A MAGNETIC COMPASS RESPONSE OF AN ORGANISM [1]

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Previously reported studies (Brown, Brett, Bennett and Barnwell, 1960; Brown Webb and Brett, 1960) have established beyond reasonable doubt that mud-snails, *Nassarius obsoleta,* are able to perceive and exhibit quantitative alterations in orientational responses to a change in the magnetic field strength amounting to about a 10-fold increase over the earth's natural one. In these studies the experimentally increased field appeared to effect predominantly the same kind of response, whether the field direction remained unaltered or was abruptly rotated through 90° in a horizontal plane. The size of the response to the change in strength of field, and in some measure also the character of the response, were clearly functions of phases of both solar and lunar periods. The response was one of graded amounts of clockwise or counterclockwise turning in the magnetic field.

If orientation in a magnetic field were to be a phenomenon of a useful nature in spatial orientation and navigation, it would be expected that the organism would exhibit a capacity to distinguish the directions of lines of magnetic force as indicated by differential responses to fields at right angles to one another. Suggestion that this might be the case has been reported (Brown, Webb, Bennett and Barnwell, 1959). The following is an analysis to determine whether the snails actually possess such a capacity to respond differentially.

Method

The apparatus and methods for obtaining the data have been reported earlier (Brown, Brett, Bennett and Barnwell, 1960). In essence, the experiments comprised permitting snails to emerge from a magnetic-south-directed, straight, narrow corridor into a constant, symmetrical field provided with a grid such that the mean amount of right or left turning during the initial 3 cm. of free movement could be assayed. Each experimental series consisted of two samples of ten passages in the earth's field, two samples of ten in an experimentally increased field oriented as the earth's, and two samples of ten in an increased field rotated 90° clockwise from the natural. The order of the groups of ten in the series of 60 was scrambled except the first three groups of ten in nearly every instance consisted of one with each field, as did also the second of the three groups of ten. Between June 28 and August 29 a total of 564 series of 60 snail runs was obtained between the hours of 5 AM and 9 PM. Though only 17 hours of the solar-day were represented by the data, all hours of a lunar day and all days of a natural synodic month were represented. The number of series for single solar-day hours ranged from 9 to 50, for single lunar-day hours from 5 to 22 and for the single

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days of a natural semi-monthly period (15-day periods synchronized to new and full moon) from 3 to 37.

Results

A daily rhythm was found in the relative effectiveness on the orientation of the snails of the two magnetic fields oriented at right angles to one another. This

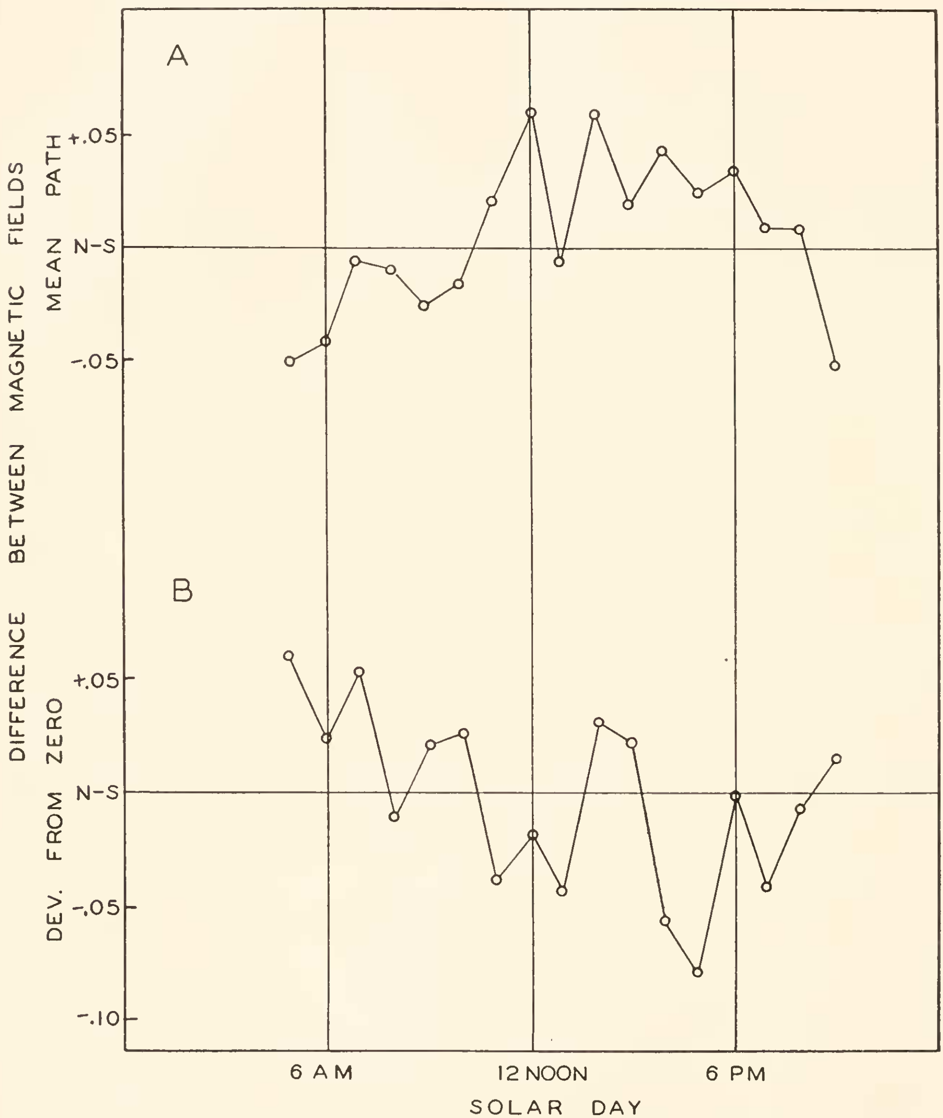

FIGURE 1. A. The drift through the solar-day of the effectiveness of the E-W magnet field relative to the N-S field in producing mean path difference from controls. B. Same as for A, except for being relative effectiveness in producing dispersion of paths from zero, irrespective of sign.

was demonstrated first for the amount of induced turning of snails in the experimental magnetic fields expressed as difference between the responses of the snails in these fields and the controls in the same series. In Figure 1A is shown the systematic fluctuation in effectiveness of the East-West (E-W) magnetic field relative to the North-South (N-S) field. In the early morning (5–6 AM) the E-W field is the more effective in producing counterclockwise turning of the snails; this is followed by a gradual drift to a time shortly after noon when the N-S field is more effective in producing comparable turning, whereafter, there is a gradual return to a greater effectiveness of the E-W field in the evening. A correlation between the relative effect of the two magnetic fields and the hour angle of the sun expressed as deviation from 2:30 PM (+37.5°) yielded a coefficient of 0.794 ($N = 17$; $P < 0.001$).

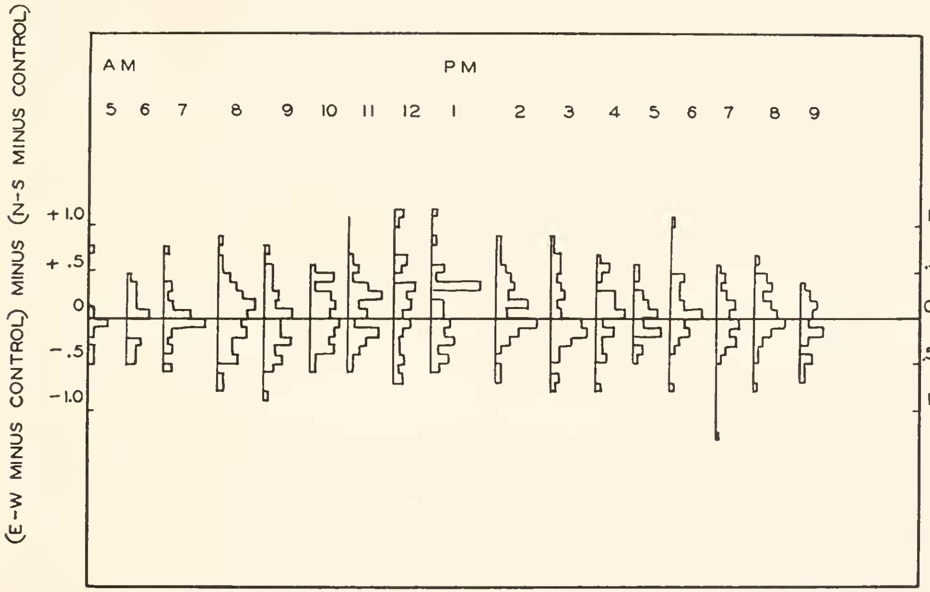

FIGURE 2. Frequency distributions, as a function of hour of day, of the differences between effectiveness of the experimental E-W and N-S fields in altering mean path from the control one.

A comparable daily rhythm was also seen in the difference between the responses to the two magnetic fields in effecting alterations in the total dispersion of pathways, both clockwise and counterclockwise. In Figure 1B it is seen that the E-W field is more effective in producing dispersion of pathways in the early morning, whereas the N-S field tends gradually to become more effective until late afternoon when the relationship seems to reverse again. When this relationship of the two magnetic fields is examined as a linear correlation with the hour angle of the sun expressed as deviation from 4:30 PM (+67.5°), a coefficient of 0.664 is found ($N = 17$; $P < 0.005$).

A daily rhythm in the response as measured by dispersion of paths, or total turning response to magnetic field, whether clockwise or counterclockwise, is perhaps more evident in Figure 2, in which the frequency distributions of the

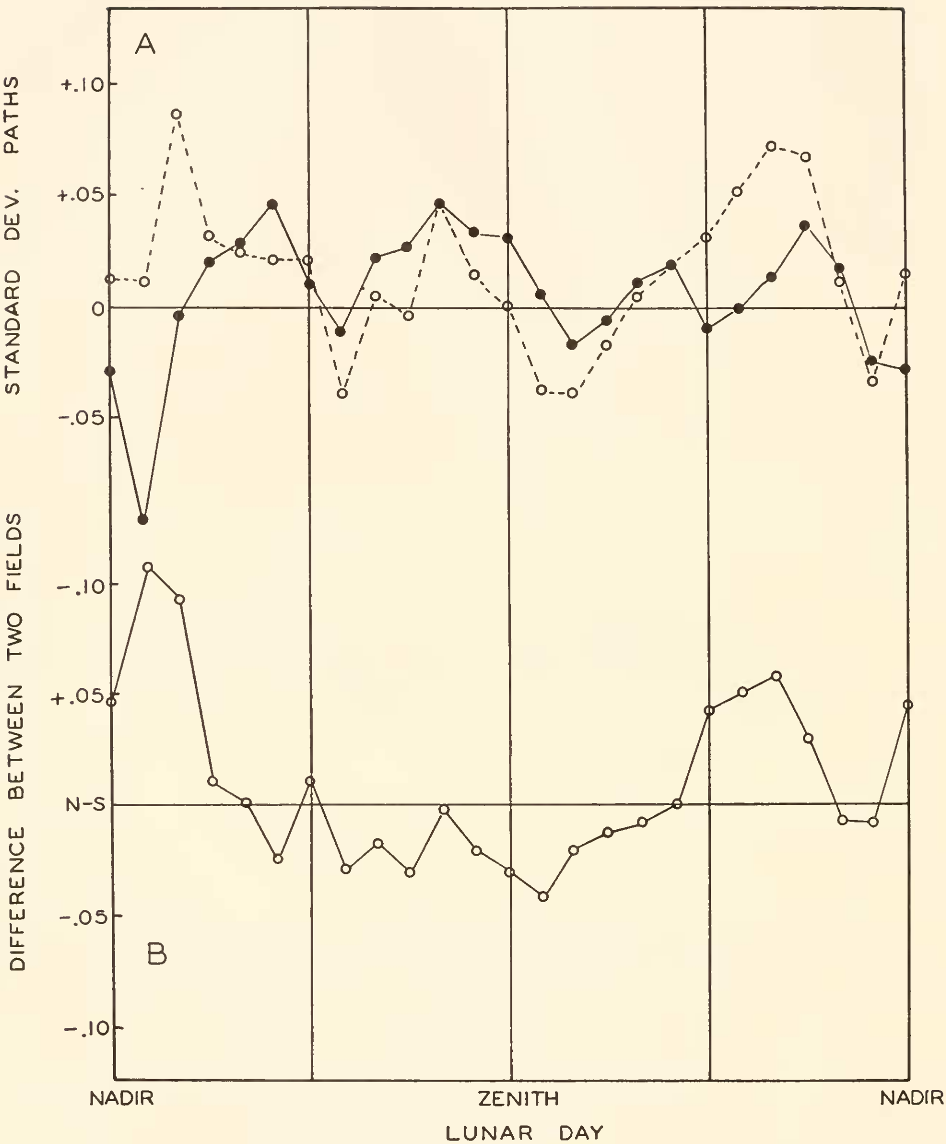

FIGURE 3. A. The difference of the standard deviations for snails in the E-W (dashed line) and N-S (solid line) fields from standard deviation of the controls as a function of hour of lunar-day. B. Drift through the lunar-day of the effectiveness of the E-W field relative to the N-S one in altering standard deviation from that of the controls. Points are calculated from three-hour grouped data.

differences between the responses to the two magnetic orientations are shown as functions of the hours of the solar day. Study of this figure reveals a tendency towards unimodality of distributions in the early morning and evening, with greater dispersion and a definite tendency toward bimodality during the middle of the day. This daily difference between the responses to the two magnetic fields can be demonstrated to be statistically probable beyond reasonable doubt by comparing standard deviations of the distributions. For example, the values for 5–10 AM, 11 AM to 3 PM, and 4–9 PM are, respectively, 0.308 ± 0.0158, 0.389 ± 0.01935, and 0.322 ± 0.0166. The difference between the first and second is 0.081 ± 0.0250 ($t = 3.24$; $N = 394$), and between the second and third 0.068 ± 0.0255 ($t = 2.64$; $N = 391$). As would be expected were this daily rhythm of dispersion a consequence of a mirror-imaging response to the two magnetic fields, differences and their significance can be substantially increased by taking samples for shorter periods symmetrically arranged over the daily period. For example, selecting the three periods, 5–7 AM, 11 AM–1 PM, and 5–7 PM, one obtains values for standard deviations as follows: 0.276 ± 0.0263, 0.413 ± 0.0272, and 0.276 ± 0.0221. Differences between first and second and second and third are, respectively, 0.137 ± 0.0379 ($t = 3.62$; $N = 173$) and 0.137 ± 0.0351 ($t = 3.91$; $N = 196$), differences which are statistically significant beyond all reasonable doubt ($P < 0.001$).

Hence, it is quite evident that the two magnetic fields are being distinguished by the snails, maximally so over the noon hour, and gradually decreasingly so during approximately the preceding and succeeding six-hour periods.

A lunar-day fluctuation in the difference between the dispersion effected by the two positions of the magnet is also evident. This dispersion is indicated here as standard deviation. Using only the 30-day period, July 6-August 4, when the daily series were the most complete and therefore the solar-daily cycle most fully randomized, the relationship between hour of the lunar-day and the magnetic effect expressed as difference from simultaneous control is shown in Figure 3A. The relative effectiveness of the two magnet orientations is plotted in Figure 3B. In view of the differing sizes of the samples for the various lunar-day hours and days of synodic month, these values were calculated as grouped data for overlapping three-hour periods of the lunar day. The results suggest strongly that the E-W field is relatively the more effective during the hours the moon is below the horizon, and the N-S field during the hours the moon is above the horizon. The N-S field is relatively more effective in inducing dispersion just after lunar zenith, becoming progressively less so both as one proceeds to earlier or later hours of the lunar-day. The E-W magnetic field is most effective just after lunar nadir. There is a suggestion of a brief period of greater effect of the N-S field just preceding lunar nadir. This lunar-day cycle displays a qualitatively comparable relationship of the relative effects of the two fields to that seen for the the corresponding hours of the solar day (see Figure 1B).

A very high statistical significance for the lunar-day cycle of relative effectiveness of the two magnetic fields was demonstrated by finding a coefficient of correlation of 0.752 ($N = 20$; $P < 0.001$) between the difference between the two fields and the hour angle of the moon expressed as deviations from −22.5°, through a total of ±11 hours. For this correlation, the individual lunar-day hourly values, of course, were used rather than the three-hour moving means.

However, during a four-hour period of the lunar-day represented by too few experimental series, the data were combined into two two-hour periods, hence the N of 20 instead of the expected 22.

Using data grouped for three-hour periods it was found that there was a complex lunar-day periodism in the difference between the effectiveness of the two magnet orientations in determining mean snail path. This comprised maximum action by the E-W field in causing left-turning one to two hours after lunar-nadir, and maximum left-turning effect of the N-S field between the times of moon-set and nadir (Fig. 4). Superimposed on this last cycle was a lunar-tidal cycle in which a conspicuous, but secondary, increased effectiveness of the E-W

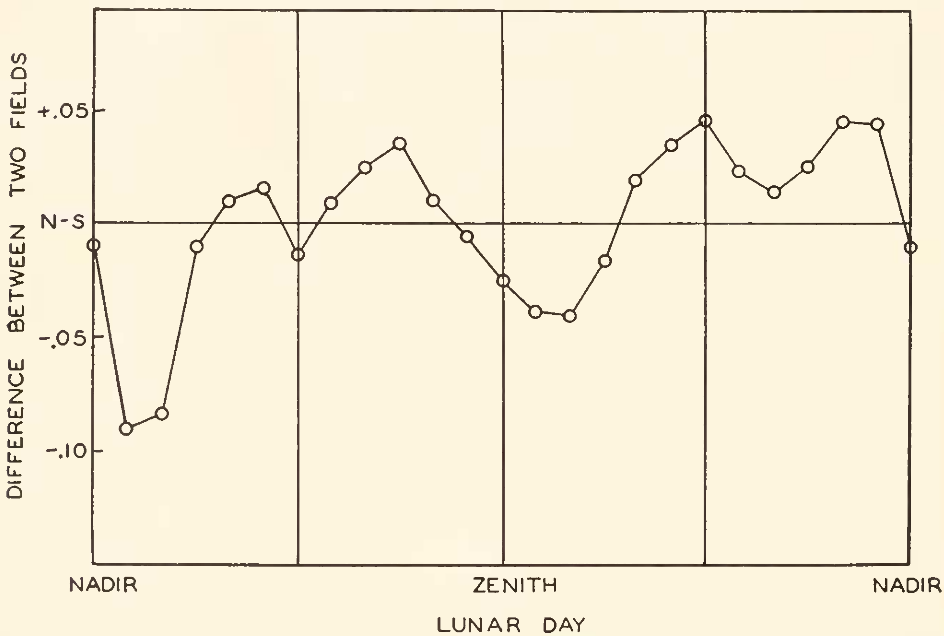

FIGURE 4. The drift through the lunar-day of the effectiveness of the experimental E-W relative to the N-S field in altering mean path from the control one. Points are calculated from three-hour grouped data.

field occurs one to two hours after lunar zenith. There is also a suggestion that this bimodal lunar-day, or lunar-tidal, fluctuation in the relative effects of the two magnetic fields possesses still a further, and lesser, harmonic to give a quadri-modal lunar-day cycle.

It was shown earlier (Brown, Webb and Brett, 1960) that there was, during the two-month period of study, a semi-monthly cycle of direction and degree of turning of the snails induced by the magnets with maximum clockwise turning a day or two before new and full moon, and maximum counterclockwise turning just before the times of first and third quarters of the moon. When now the actions of the two experimental magnetic fields were compared for their contribution to this semi-monthly rhythm, it was found that the two magnetic orientations

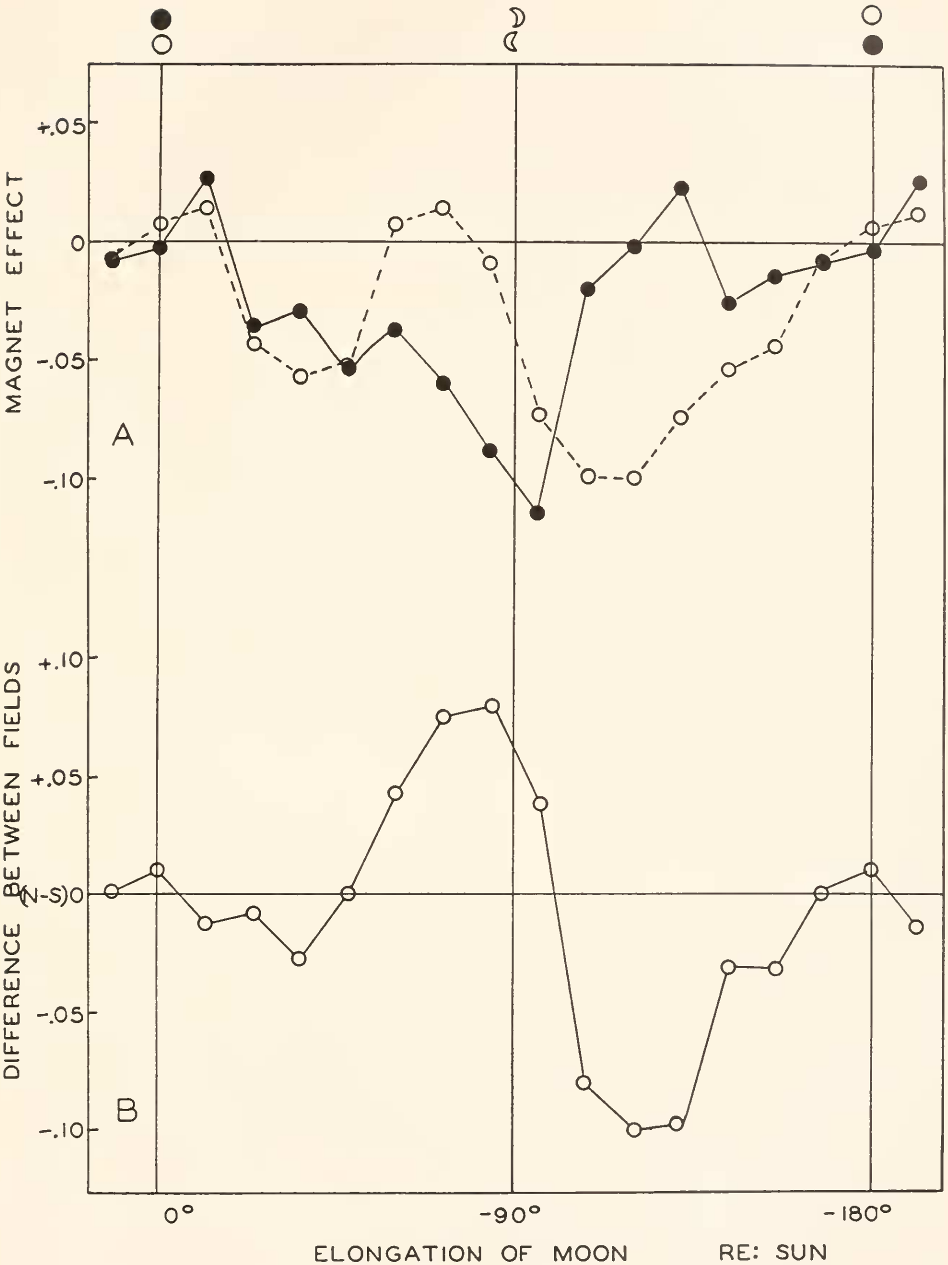

FIGURE 5. A. The drift through the semi-monthly period of the difference between the mean path of snails in the E-W (dashed line) and N-S (solid line) fields from that of the control snails. B. The drift through the semi-monthly period of the effect of the E-W magnetic field relative to the N-S one, in influence on mean snail path. Points are calculated from three-day grouped data.

produced quite strikingly different semi-monthly patterns of effectiveness (Fig. 5A). The difference between them is illustrated in Figure 5B. The E-W field produced relatively a much greater counterclockwise turning about two to four days before the lunar quarters, and then there occurred a very rapid reversal resulting in the N-S field having comparably greater counterclockwise turning action immediately after the lunar quarters. These semi-monthly relationships were computed as overlapping three-day groupings of all data to compensate for greatly differing numbers of series representing the various semi-monthly days.

Discussion

It is evident that the two magnet positions, one with lines of force at right angles to the other, while appearing very similar in effect in indiscriminately pooled data, are in fact not equivalent for the snails at all times of solar and lunar periods. This has been established by the demonstration that the relative effectiveness of the two in inducing left-turning alone, and in affecting total dispersion of pathways (both left and right) exhibit systematic fluctuations through the solar-day, lunar-day and synodic month. In the solar-day, the two fields become essentially equivalent about 8–9 AM and 8–9 PM with difference between the two, in general, increasing systematically during the hours involved in this study as one moves away from these times into the intervening daily hours. For the solar daily cycle, snails moving toward magnetic south in the early morning hours are more strongly turned eastward in an increased magnetic field of E-W orientation than in one oriented 90° to it. On the other hand, by noon, it is the N-S oriented magnet which turns them more strongly eastward. Comparably, in total turning, both eastward and westward, it is the E-W oriented field which produces most turning in the early morning and the N-S field which is most effective from noon to late afternoon. In the daily cycle of response, the snails behave as if they possessed a horizontal directional magnetic axis detector turning through the day like an "antenna."

When the data were rearranged to become lined up in terms of hours of a lunar-day, a quite similar systematic fluctuation was seen, now with the E-W magnetic field exerting the greater turning, either east or west, when the moon was below the horizon, and the N-S field, during the time the moon was above the horizon. This relationship is essentially comparable to the corresponding solar-day one, but the particular phases appear to occur slightly earlier. In this lunar-day fluctuation of the relative influence of the two fields, where all hours of the lunar-day are represented, there is a slight suggestion of a bimodality of the lunar daily cycle with a second, very brief, period of greater effect of the N-S magnet occurring just before lunar nadir.

Although the semi-monthly cycle of the relative effects of the two fields may be at least in some measure an artifact which is a consequence of exclusively daytime sampling, it does lend striking confirmation to the solar-day and lunar-day studies in demonstrating the physiological non-equivalence of the two magnet positions as a function of time.

There seems too little information available to formulate any hypothesis as to how this capacity for magnetic response, so clearly tied in with the fundamental "clock system," might normally operate in orientation of the snail. Orientation in snail populations may occur to some extent by a magnetoklinokinesis, in which the snails would tend on the average to assume a specific orientation at particular times of day as a consequence of different turning responses for different magnetic orientations, relative to the body axis. However, the clear demonstration that snails can also respond to fields by predominantly either left or right turning, again depending upon time, and can differentiate between two magnetic fields, leaves open the possibility that under some conditions, or at some times of their lives, behavioral response of the snails may possess less the character of a klinokinesis and, instead, more that of a clock-regulated taxis, or even a straightforward compass reaction. The demonstration that in one species, there is a clear clock-regulated capacity to orient in a weak magnetic field and to distinguish directions of magnetic lines of force encourages one to postulate that this fundamental capacity may have become associated with highly evolved and specialized mechanisms in species with unusual homing or other navigational capacities.

In the solar-day and lunar-day cycles of difference between the response to the E-W and N-S fields, the snails are behaving quite as if in their response to magnetic field they were to a small but significant extent slaves of magnetic compass needles within their bodies, with these individual compass needles in turn being hands on two kinds of horizontally oriented clocks, solar-day and lunar-day. Some modification of such a compass response might be expected were the well-known "sun-compass" and "moon-compass" orientations of organisms, with their continuous correction for rotation of the earth, dependent in any way upon a continuously altering relationship of the position of these heavenly bodies relative to the direction of the earth's magnetic lines of flux. This might constitute the regulator of the gradually altering sun-compass or moon-compass angle of orientation of the organisms.

It is, of course, common knowledge that to localize the position of the sun or moon which for one or another reason is not immediately visible, it is not sufficient to have only an accurate record of time. One needs an additional parameter, one indicating spatial orientation on the earth's surface. This could not be better nor more directly provided for than through a general organismic capacity for distinguishing direction in terms of the natural magnetic lines. The possession of "living compasses" along with "living clocks" could therefore constitute a potential means for organismic navigation in the absence of more obvious cues.

This demonstrated capacity for differentiating between the directions of the two experimental magnetic fields, since it deals with a weak field strength relatively close to that of the earth's natural one, reinforces still further the earlier conclusions (Brown, Brett, Bennett and Barnwell, 1960; Brown, Webb and Brett, 1960) that the observed solar and lunar daily fluctuations in orientations by the snails in the earth's natural magnetic field and otherwise in a field symmetrical with respect to all previously recognized orienting factors, are at least in part a true orientation in response to that magnetic field.

Summary

1. The snail is able to differentiate between two weak magnetic fields, one oriented at right angles to the other.

2. The relative influence of experimental north-south and east-west oriented magnetic fields in producing dispersion of snail pathways, or effecting a magneto-klinokinesis, displays both solar- and lunar-day rhythms.

3. The relative influences of experimental N-S and E-W fields in effecting a predominantly counterclockwise snail-turning exhibits solor daily, lunar daily, and semi-monthly rhythms.

4. The solar and lunar clock-regulated discriminatory responses for magnetic fields indicate the snail to be significantly oriented as if by internal magnetic compass needles which in turn are hands of horizontal solar- and lunar-day "clocks."

5. Further arguments are advanced for concluding that organismic orientation to the earth's natural weak magnetic field is a normal organismic phenomenon.

6. Implications of this demonstrated solar and lunar "clock-compass" capacity for the well-known "sun-compass" and "moon-compass" orientations of animals are discussed. Also, the insurance value of a "clock-compass" capacity as a potential navigational system for animals when deprived of celestial references, is pointed out.

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